The University of Chicago

DISTRIBUTION OF ANT SPECIES IN THE CHICAGO REGION WITH REFERENCE TO ECOLOGICAL FACTORS AND PHYSIOLOGICAL TOLERATION

A DISSERTATION SUBMITTED TO THE FACULTY OF THE DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

1934

By
MARY TALBOT

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DISTRIBUTION OF ANT SPECIES IN THE CHICAGO REGION WITH REFERENCE TO ECOLOGICAL FACTORS AND PHYSIOLOGICAL TOLERATION

MARY TALBOT

Whitman Laboratory, University of Chicago

ECOLOGICAL SURVEY

Introduction[1]

This study of the distribution of ants was made within a radius of ninety miles of Chicago in a number of available communities. The oak-hickory and beech-maple woods contain an essentially northeastern fauna while the prairies bring in western forms and the dunes contribute a few distinctly southern species.

The purpose of the work was two fold: (1) to make a survey of the ant distribution of the area, correlating this distribution with the recognized plant communities and (2) to make certain experimental studies with reference to the toleration of ants to extremes of heat and dryness in order to ascertain whether these could be shown to be limiting factors in distribution. In most of the work ants of one genus were used in order to determine whether adaptive differences could be demonstrated between species.

Ants were studied in the various recognized stages of plant associes to ascertain, not only the distribution of various species, but to determine whether this distribution fits that of the plant communities. It is believed that if sufficient groups of animals: ants, spiders, snails, mammals, etc., are studied through the steps of ecological succession, and if these studies are later gathered together, as complete a picture of animal succession may be shown for the region as has already been described for the plants. Ants are especially favorable animals for this study because they are abundant in numbers (but do not have so many species as to complicate the work too much), their nests are permanent over a number of years and are found in fairly definite habitats, and ants of one species or another occupy almost every niche. In addition, W. M. Wheeler ('32) states that, "Ants are so extremely sensitive to the degrees of temperature and humidity of their environment and to the character of its vegetation that many species or subspecies are confined to very narrow ecological habitats."

[1] Identifications of most of the ants were kindly checked by Dr. M. R. Smith; *Myrmica* by Dr. Neal Weber. I wish also to express my appreciation for help from Dr A. E. Emerson, Dr. C. H. Kennedy and Dr. W. C. Allee.

Ants were collected (table I) over a period of three years from the following locations:

(1) The dunes of the south and southeast shores of Lake Michigan at such places as Miller, Ogden, Tremont and Furnaceville, Indiana; and Lakeside, Michigan; (2) Oak woods on moranic clay at Palos Park and New Lennox, Illinois; and Valparaiso, Indiana; (3) Beech-maple climax woods at Joliet, Illinois; Smith and Turkey Run, Indiana; and Warrens Woods and Lakeside, Michigan; (4) Prairie southwest of Chicago; (5) Roadsides and pastures at various places. Turkey Run, in central Indiana, is south of this general range but no species are included from there which are not also found in one of the more northern locations.

General Description of the Region

The area can be divided roughly into three main successions according to the nature of the substratum: sandy deposits along southern Lake Michigan; upland moranic clay laid down by glaciers; and the prairie soil to the southwest. The dunes show a clear-cut succession from the early pioneer stages of fore-dunes, poplar dunes, and pines, through the black oak and red-white oak associes, to the beech-maple climax. On clay the majority of the woods are in some stage of oak succession. This is typically a red-white oak associes merging into oak-hickory in some places. This succession also leads to a beech-maple climax. Prairie reaches almost its eastern limit here and is not extensive. It is the climax condition, passing through stages of bog and low prairie.

Plant successions for the region have been unusually well worked out (Cowles, '01, and Fuller, '25); animal communities have been studied to a less extent (Shelford, '13, Holmquist, '26, Park, '30, and Pearson, '33); and some valuable environmental data have been recorded (Fuller, '14, and Park, '31).

Distribution

Extensive sand dunes have been formed along the southern shores of Lake Michigan. Near the lake the sand ridges are still in a very unstable condition. Moving dunes and blowouts are common but in most places the dunes are caught and held by sand-binding grasses, shrubs, and poplar trees. Further back the dunes become stable and thoroughly wooded, first with pines, then with oaks. This makes an unusually clear-cut succession of ecological habitats and gives an exceptional opportunity for correlating distribution with environmental differences (fig. 1).

Beach.—The flat beach consists of almost bare sand with a few pioneer herbaceous plants forming a sparse vegetation. Ants cannot become established here.

Fore dunes.—Behind the beach the fore dunes rise fifteen or twenty feet. They are out of reach of even winter storm waves and so can begin to acquire

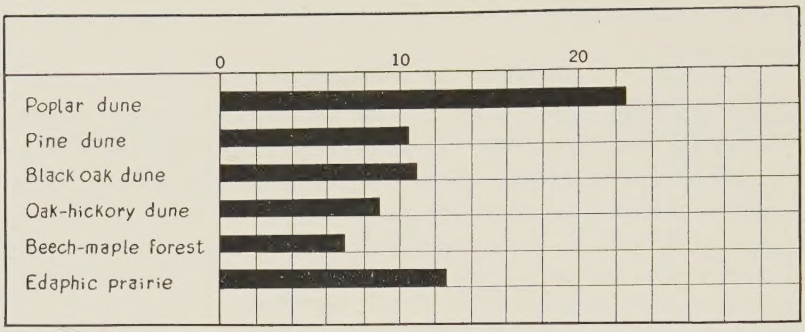

FIG. 1. Comparative mean average daily evaporation in plant communities of Chicago area (modified from Fuller, '14).

a permanent vegetation. Such xeric plants as the sand grasses (*Calamovilfa longifolia* Hack and *Ammophila arenaria* Link), bushy willows (*Salix* sp.) and the sand cherry (*Prunus pumila* L.) tend to hold the sand in some places. But even in patches of sand cherry and willow the sand is blown about to considerable extent. In bare areas it is being almost constantly shifted.

The fore dunes are not a very suitable place for ants, partly because of this instability. Ant nests are maintained for a number of years and usually depend upon a stable substratum. Great extremes of temperature and moisture and lack of diversity of food and habitat are also limiting factors in the fore dunes. Sand is the only habitat which may be relied upon to be present and so the characteristic ants of the fore dunes are the crater-forming *Lasius niger neoniger* and *Pheidole bicarinata.* Colonies are not common and exist only near the roots of grasses or sand cherry and are usually found on slopes away from the lake, which is on the windward side. In addition to these species, an occasional pioneer colony of log dwelling ants can be found. A log offers great protection and minimizes extremes of temperature and dryness. It may be noted also that the two species found are both widespread. It seems that *Camponotus herculeanus pennsylvanicus* can exist wherever large solid logs are found and *Camponotus caryae,* while not a common ant, is also widespread (table I).

In general, species of ants occupying habitats in which there are severe conditions may be divided into two types: those which face their environment and are adjusted to withstand great extremes of heat and dryness, and those which avoid these extremes. The two ants characteristic of the fore dunes are of the latter type. On hot dry days they will be found quietly aggregated several inches below the surface of the sand, emerging only in the cool of the evening, or where the shade keeps the sand surface below the critical temperature.

The nature of sand causes it to hold water to a marked degree. The action of wind on sand causes a dry mulch three to five centimeters thick to be formed (Fuller, '14). This protects the layer beneath, consequently sand

here rarely dries out to the extent and depth of clay or loam and the ants are able to make use of this to exist under conditions which would otherwise be prohibitive.

Poplar dunes.—Behind the fore dunes there is typically a large depression of almost bare sand. Beyond this the poplar dunes rise fifty or more feet on the second series of ridges back from the lake. This ridge is larger than that of the fore dunes and is characterized by scattered clumps of poplars (*Populus deltoides* Marsh). There are also frequent patches of red-osier dogwood (*Cornus stolonifera* Michx.), in addition to the sand cherry, willows, and bunch-grass of the fore dunes.

Conditions of temperature and moisture are essentially those of the fore dunes. Poplars result in a slight addition to the food supply but habitats still consist of bare sand and an occasional log. The instability is still great but there are larger areas of sand held by roots of dogwood and grasses so that the number of *Lasius* and *Pheidole* nests increases greatly. These are again the characteristic ants, with the *Camponotus* group as the only other representative, except an occasional *Formica pallide-fulva schaufussi* which wanders in from the pines.

The way in which ants can avoid extremely high temperatures by going beneath the surface is shown by some of Shelford's ('12) records for the poplar dunes. One summer day when the air temperature was 36° C., that of dry sand 1.25 cm. below the surface was 47° C., while moist sand at that level was only 32° C. At 8 or 9 cm. below the surface moist sand was 29° C. and at 12 or 13 cm. it was 27° C. An ant walking on the surface would have to face a temperature of 47° C. with its accompanying low humidity, while an ant 8 or 9 cm. beneath the surface would face no extremes of heat or dryness. At Whitman Laboratory, on June 10, 1933, it was noted that *Lasius niger neoniger* ants were actively going in and out of craters in the shade while nearby craters in the sun showed no activity. It was found that the sand surface temperature in the sun was 48° C. while eight feet away in the shade the sand surface temperature was only 29° C.

Pine dunes.—Behind the poplars there is usually another smaller depression. From this the more extensive pine dunes rise. Here poplar trees and their accompanying plants have lived and died adding some humus to the sand and binding it with their roots so that a suitable place for pine seedlings is provided. With the pines (*Pinus banksiana* Lamb. and *P. strobus* L.) are found junipers (*Juniperus* sp.), patches of bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), aromatic sumac (*Rhus canadensis* Marsh) and many more of the xeric herbaceous plants. The area has a distinctly evergreen aspect.

Extremes of heat and dryness are cut down to marked degree in the pines. Evaporation is only about half that of the poplar dunes (fig. 1). The slight mixture of humus in the sand seems to be decidedly favorable for several species of ants although the water content of the sand is somewhat less than in

TABLE I. *Ant distribution in the Chicago Area. S = nesting in soil. SL = using soil and log. L = using log*

	Fore Dunes	Poplar Dunes	Pine Dunes	Black Oak on Sand	Red-White Oak on Sand	Mixed Oak on Clay	Oak-Maple on Sand	Beech-Maple Climax	Prairie	Pasture	Stages in Log Succession
1. *Stigmatomma pallipes* Hald.	—	—	—	L	—	L	L	—	—	—	4, 5
2. *Ponera coarctata pennsylvanica* Buck.	—	—	—	L	L	L	L	L	—	S	2, 3, 4, 5, 6
3. *Stenamma brevicorne* Mayr	—	—	—	—	L	L	L	L	—	—	
4. *Aphaenogaster treatae* Forel	—	—	—	S	S	—	—	—	—	—	
5. *Aphaenogaster fulva* Roger	—	—	—	L	—	L	L	L	—	—	4, 5, 6
6. *Aphaenogaster fulva aquia* Buck.	—	—	—	L	L	L	L	L	—	S	3, 4
7. *Aphaenogaster fulva aquia* var. *picea* Emery	—	—	—	—	L	L	L	L	—	—	3, 4, 5, 6
8. *Aphaenogaster tennesseensis* Mayr	—	—	—	—	—	L	L	L	—	—	2, 3
9. *Myrmica punctiventris* Roger	—	—	—	—	—	S	—	—	—	—	
10. *Myrmica scabrinodis brevinodis* var. *sulcinodoides* Emery	—	—	—	—	—	S	S	—	—	—	
11. *Myrmica scabrinodis schencki* var. *emeryana* Forel	—	—	SL	SL	SL	S	S	S	—	—	
12. *Myrmica scabrinodis lobicornis* var. *fracticornis* Emery	—	—	—	—	—	S	—	—	—	—	
13. *Pheidole pilifera* Roger	—	S	—	—	—	—	—	—	—	S	
14. *Pheidole bicarinata* Mayr	S	S	S	S	—	—	—	—	—	—	
15. *Pheidole vinelandica laeviuscula* Emery var.	—	—	S	S	—	—	—	—	—	—	
16. *Crematogaster lineolata* Say	—	—	L	L	—	L	—	—	—	SL	2, 3, 4
17. *Crematogaster lineolata* var. *cerasi* Fitch	—	—	—	—	L	L	—	L	—	S	2, 3, 4
18. *Monomorium minimum* Buck	—	—	S	S	S	—	—	—	—	—	
19. *Monomorium pharaonis* L.	Chicago—hospital and house.										
20. *Solenopsis molesta* Say	—	—	—	SL	SL	S	—	S	S	S	
21. *Myrmecina graminicola americana* Emery	—	—	—	—	—	L	L	L	—	—	4, 5
22. *Leptothorax fortinodis* Mayr	—	—	—	—	—	L	—	—	—	—	
23. *Leptothorax longispinosus* Roger	—	—	—	—	—	L	L	L	—	—	
24. *Leptothorax curvispinosus* Mayr	—	—	—	L	L	L	L	L	—	—	
25. *Leptothorax curvispinosus ambiguus* Emery	—	—	—	—	—	S	—	—	—	S	
26. *Leptothorax texanus* Wheeler	—	—	S	S	—	—	—	—	—	—	
27. *Dolichoderus plagiatus* Mayr	—	—	—	—	—	S	—	—	—	—	
28. *Dolichoderus plagiatus pustulatus* Mayr	Sphagnum bog, Volo, Ill.										
29. *Tapinoma sessile* Say	—	—	—	L	L	L	—	L	—	L	2, 3, 4
30. *Iridomyrmex humilis* Mayr	University of Chicago, Zoology Building										
31. *Iridomyrmex pruinosis* var. *analis* André	—	—	S	—	—	S	—	S	—	—	
32. *Brachymyrmex heeri* var. *depilis* Emery	—	—	—	—	—	—	—	—	—	—	
33. *Camponotus castaneus* Lat.	—	—	SL	SL	—	SL	—	SL	—	—	
34. *Camponotus castaneus americanus* Mayr	—	—	—	—	—	—	—	—	—	—	
35. *Camponotus herculeanus pennsylvanicus* De Geer	L	L	L	L	L	L	L	L	—	L	2, 3, 4
36. *Camponotus herculeanus pennsylvanicus* var. *ferrugineus* Fabr.	—	—	—	—	—	L	—	L	—	L	2, 3, 4
37. *Camponotus herculeanus ligniperdus* var. *noveboracensis* Fitch	—	—	L	L	—	—	—	—	—	—	2, 3, 4
38. *Camponotus caryae* Fitch	L	L	—	L	—	L	L	—	—	L	3
39. *Camponotus caryae* var. *minutus* Emery	—	—	—	—	—	L	—	L	—	SL	3
40. *Camponotus caryae subbarbatus* Emery	—	L	—	—	—	L	—	—	—	—	
41. *Camponotus caryae discolor* Buck.	—	—	—	—	—	L	—	—	—	—	3
42. *Camponotus caryae* var. *tanquaryi* Wheeler	—	—	—	—	—	L	—	—	—	—	

TABLE I (*continued*)

	Fore Dunes	Poplar Dunes	Pine Dunes	Black Oak on Sand	Red-White Oak on Sand	Mixed Oak on Clay	Oak-Maple on Sand	Beech-Maple Climax	Prairie	Pasture	Stages in Log Succession
				Botany Greenhouse, University of Chicago.							
43. *Paratrechina* (*Nylanderia*) *parvula* Mayr	—	—	S	S	—	—	—	—	—	—	
44. *Paratrechina* (*Nylanderia*) *vividula guatemalensis* Forel	—	—	S	S	—	S	—	—	—	—	
45. *Prenolepis imparis* Say	—	—	S	S	—	—	—	—	S	S	2, 3, 4
46. *Prenolepis imparis* var. near *testacea* Emery	S	S	S	S	SL	S	L	L	S	S	2, 3, 4, 5, 6
47. *Lasius niger* var. *neoniger* Emery	—	—	—	L	L	SL	L	L	S	S	4, 5, 6
48. *Lasius niger alienus* var. *americanus* Emery	—	—	—	—	L	L	L	L	—	—	3, 4, 5, 6
49. *Lasius flavus nearcticus* Wheeler	—	—	—	—	—	L	—	—	—	S	
50. *Lasius umbratus mixtus* var. *aphidicola* Walsh	—	—	—	—	—	—	—	—	—	—	4
51. *Lasius umbratus mixtus* var. *speculiventris* Emery	—	—	—	—	L	L	L	—	—	—	
52. *Lasius* (*Acanthomyops*) *claviger* Roger	—	—	—	—	—	S	—	S	—	—	
53. *Formica sanguinea subintegra* Emery	—	—	—	—	SL	S	—	—	—	S	
54. *Formica sanguinea rubicunda* Emery	—	—	—	—	—	S	—	—	—	—	
55. *Formica sanguinea subintegra* Emery	—	—	—	—	—	S	—	—	—	—	
56. *Formica sanguinea subnuda* Emery	—	—	—	S	S	—	—	—	—	S	
57. *Formica truncicola obscuriventris* Mayr	—	—	—	—	—	S	—	—	—	S	
58. *Formica exsectoides* Forel	—	—	—	—	—	S	S	—	—	S	
59. *Formica ulkei* Emery	—	—	SL	SL	SL	SL	SL	SL	—	S	
60. *Formica fusca* var. *subsericea* Say	—	—	—	—	—	—	—	—	S	S	
61. *Formica fusca* var. *subaenescens* Emery	—	—	—	—	—	—	—	—	—	S	
62. *Formica cinerea* var. *neocinerea* Wheeler	—	—	—	—	—	—	—	—	—	S	
63. *Formica neogagates* Emery	—	—	—	—	—	—	—	—	—	S	
64. *Formica neogagates lasioides* var. *vitula* Wheeler	University of Chicago campus.										
65. *Formica pertinax* Wheeler n. var.	—	SL	SL	SL	SL	S	—	—	—	S	
66. *Formica pallide-fulva schaufussi* Mayr	—	—	SL	SL	SL	S	—	—	—	S	
67. *Formica pallide-fulva schaufussi* var. *incerta* Emery	—	—	SL	SL	SL	S	—	—	S	S	
68. *Formica pallide-fulva nitidiventris* Emery	—	—	—	SL	SL	S	—	—	—	S	
69. *Formica pallide-fulva nitidiventris* var. *fuscata* Emery	—	—	—	—	—	—	—	—	S	—	
70. *Polyergus rufescens breviceps* Emery	S, 2 SL, – L, 2	S, 3 SL, 1 L, 3	S, 9 SL, 6 L, 3	S, 10 SL, 8 L, 11	S, 3 SL, 8 L, 11	S, 20 SL, 3 L, 23	S, 3 SL, 1 L, 14	S, 4 SL, 2 L, 18	S, 6 SL, – L, –	S, 19 SL, 2 L, 4	
	4	7	18	29	22	46	18	24	6	25	

the poplars (Fuller, '14). Several habitats are offered: open sand, sand covered with needles or a slight layer of leaves, logs, and even the decayed parts of living trees. Food is more abundant and more varied because of the greater variety of plants and an increase in the number of insects.

Of the eighteen species collected in the pines, nine live in the open sand with no shelter, six require sand with some sort of protection above it (logs, bark, needles) while three are characteristic log-inhabiting forms. Of the species nesting in sand two (*Pheidole bicarinata* and *Iridomyrmex pruinosus analis*) are characteristic of sand and seem confined to it. *Monomorium minimum, Paratrechina* (*N.*) *parvula,* and *Lasius niger neoniger* are able to live on bare clay but are more abundant in sand. All of these are eliminated very quickly by a covering of vegetation over the ground, so it would seem that lack of an open substratum is a decided limiting factor in these cases.

An important new element in the pine area is the *Formica pallide-fulva* group. All four of its northern subspecies and varieties are represented. This group and the *Camponotus* members stand out in contrast to the other ants in the pines in that they are adapted to the region in such a way that they meet and withstand extreme environmental conditions. On very hot summer days these two genera are often the only ants seen at the surface—the others are hidden away in the moist sand several inches below the surface.

The southern forms, *Iridomyrmex pruinosus analis* and *Leptothorax texanus* seem almost confined to the pines.

Black oak dunes.—Under the shelter of pines, in the slight humus, and the more moist and moderate conditions, seedling black oaks can start. These gradually crowd out the pine and the pine woods merges into a black oak (*Quercus vetulina* Lam.) associes. With the coming of the oaks minor plants are also crowded out or relegated to the more open places. In their place are found bush honeysuckle (*Dierville lonicera* Mill), bracken fern (*Pteris aquilina* L.), cactus (*Opuntia rafinesquii* Engelm.), lupine (*Lupinus perennis* L.), and many other shrubs and herbs. Vegetation becomes much more diverse.

In the black oaks, humus has accumulated but the soil is never very thickly covered with leaves and there are many openings which have an essentially pine flora and fauna. Temperature and moisture ranges are not much moderated from those of the pines but plants available for food and shelter have increased greatly.

Of the twenty-nine ants found, only six live in open sand. They are confined to the openings in the oaks and are crowded out where vegetation covers the woods floor. Thus, *Lasius niger neoniger* craters are very abundant in open sand but decayed logs in the deeper woods usually contain nests of *Lasius niger alienus americanus.* The relicts from the pines, *Monomorium minimum, Pheidole bicarinata,* and *Paratrechina* (*N.*) *parvula,* are quickly crowded out by leaf covering. *Aphaenogaster treatae* is not common and is usually found nesting at the base of clumps of grass.

The four *Formica pallide-fulva* subspecies and varieties are predominant in the black oaks. Their nests are numerous all through the area and all are constructed on essentially the same plan. They are invariably found under pieces of bark or branches lying lightly on rather open ground. There are one to three holes leading down, and the main chambers of the colony are located ten to fourteen inches deep in the moist, closely packed sand. *Formica pallide-fulva schaufussi* ranges into the more xeric places while *Formica pallide-fulva nitidiventris fuscata* seems the most dependent upon constant moisture conditions.

Many ants not limited to sand invade the black oaks. *Crematogaster lineolata* is very common in rather hard logs in open spots. *Myrmica scabrinodis schenki detritinodis* is frequently found nesting in the sand under sparse leaf covering. *Ponera coarctata pennsylvanica* is found under large logs where the moisture is more constant. *Solenopsis molesta* is not common but is sometimes found in and under twigs and logs. *Tapinoma sessile* will nest under bark, under paper, or in almost any kind of trash. These are all ants which are not confined to moist woods but are often found at woods margins, in fields, or along roads.

Red oak-white oak dunes.—As humus and moisture accumulate the black oaks give way to a red-white associes (*Quercus borealis* Michx. and *Q. alba* L.). There are added many more of the mesic shrubs, vines and herbs such as witchhazel (*Hamamelia virginiana* L.), flowering dogwood (*Cornus florida* L.) and wild lily-of-the-valley (*Maianthemum canadense* Deaf.). This associes differs sharply from the black oaks in that the soil is covered, in almost all places, with a thick layer of leaves and leaf mold.

Formica truncicola obscuriventris is the characteristic ant of this habitat. At times these ants may be very conspicuous when long files are moving brood and fellow workers to a new nest. The nests consist typically of runways which cut into the humus for one half to one inch beneath the heavy leaf covering. They ramify out under the leaves so that one nest may cover four or five square feet of ground.

More mesic conditions are indicated by the coming in of *Stenamma brevicorne, Aphaenogaster fulva aquia picea, Lasius flavus nearcticus* and *Lasius claviger*. Characteristic dunes species are dropping out and consequently the red oak fauna is more like that of the mixed oaks on clay than is the black oak associes. *Aphaenogaster treatae* is the only ant found in the red oaks on sand which has not been found on clay. Since the red oaks on sand have only six species not found in the black oaks and only three not found in oaks on clay it would seem that as a habitat the red oaks are not as distinct as the other two. The relationship of these may be shown by comparing the various oaks (table II). Here "distinct" means that the ant is found in one but not the other of any two habitats compared.

Mixed oak on clay.—On moranic clay the red oak-white oak associes is the most common but in some places there is a mixture of black oak, and in others

TABLE II. *Quantitative distribution of ant species in relation to oak woods and soil*

	Species Distinct			Species Distinct		Species Common to both	
	No.	%		No.	%	No.	%
Black oaks on sand	13	36.1	Red oaks on sand	6	16.7	17	47.2
Black oaks on sand	10	16.9	Oaks on clay	27	48.2	19	33.9
Red oaks on sand	3	6.1	Oaks on clay	26	53.1	20	40.8
All oaks on sand	11	19.6	Oaks on clay	22	39.3	23	41.1

hickories (*Carya* sp.) come in. The environmental conditions and the flora are essentially like the red oak associes on sand but the areas are more widespread and extend over more types of environments. For example, there may be rather dense mesic oak woods and even more moist gullies, or the oaks may form an open, almost pasture-like woods. In these extremes, not only the numbers of colonies of ants differ, but certain species may be able to exist in one and be barred from the other. With this wide diversity of environmental conditions, habitats, and niches, we would expect similar diversity in species. This has proved to be the case; in fact the number of species reaches its climax in the oaks on clay.

In contrast to the few species which depend on the sand substratum and are eliminated by its lack, there seem to be a number of species which depend on clay or clay and loam mixture and cannot penetrate sand. Considering the facts that plants for food and shelter are to a large extent the same, and that moisture and temperature conditions may be similar, it may be that the substratum is a decided limiting factor in keeping a number of ants from entering the dunes. Mound-building ants are excluded except an occasional *Formica fusca subsericea* found nesting under a log. In contrast, the crater-forming *Prenolepis imparis,* typical of yellow clay, may be found occasionally in sand. Moist sand six to twelve inches below the surface will pack to form chambers in much the same manner as clay but a mound of sand would dry out and blow away.

Prenolepis imparis is characteristic of open oak woods on clay and its craters of yellow clay pellets are very common. The ants are active latest in the fall and earliest in the spring of any local species. Chambers are located ten to twelve inches down in solid clay. Here repletes are found in large numbers and winged forms are overwintered, to fly in early spring.

Aphaenogaster tennesseensis is a typical oak woods ant which is rather widespread in its local range but is very much restricted in its nesting site. In all cases colonies have been found either in large fairly hard logs held up off the ground or, more rarely, in the upper parts of large logs lying lightly on the soil. This lack of contact with the soil is characteristic and is all the more interesting in that Wheeler ('10) states that their queen begins her colony in the nest of a variety of *Aphaenogaster fulva,* representatives of which are usually found under logs or stones in much more moist situations.

Species of *Formica* reach their highest diversity in the oaks but are usually found at the edges of woods or in clearings. This is illustrated by the findings concerning a group of 435 *Formica ulkei* mounds at Palos Park. Of these 48 per cent are located along the margin of the woods, 34.3 per cent occur in small open clearings in the interior of the woods, and 17 per cent are located in the open (Dreyer and Park, '32). None occur in dense shade and it seems probable that these ants are able to keep a clearing around their nests by killing sprouting trees and bushes.

Ants depending on leaf secretions and leaf aphids for food reach their greatest abundance in the oaks.

Oak-maple woods on sand.—Only one such transition associes (at Lakeside, Michigan) was studied, but as it gave a rather typical habitat it seemed best to include it separately. Red and white oaks mingle with sugar maple, beech, elm, basswood, and many other species. Hemlock, a remnant from glacial periods, is also present. Five-leafed ivy and wild grape climb into the trees. A lower stratum is composed of dogwood, sassafras, witch-hazel, paw-paw, and red-berried elder. The ground is covered with many kinds of spring flowers. The type of plants indicates that moisture is greater and more constant and that light is limited. The soil is basically sand but a great part of the surface bulk is made up of humus. Leaves cover the ground and many fallen logs are lying in all stages of decay.

Ant colonies are numerous but the number of species is not great. *Aphaenogaster fulva aquia picea* reaches its peak of abundance. It is found under and in almost every thoroughly decayed log lying in a moist situation. The other abundant species are principally those which also require a rather high per cent of moisture: *Stenamma brevicorne, Myrmecina graminicola americana, Lasius flavus nearcticus,* and *Formica fusca subaenescens.*

The niches are leaf covered sand loam, logs in all stages of decay, and living and dead twigs and branches. Ants requiring a solid bare substratum are excluded. In most ways the mixed oak-maple on sand associes is more like the beech-maple climax than the oaks.

Beech-maple association.—This is the climax association toward which all woods on sand or clay are progressing. In the typical beech-maple woods the large old trees give a dense shade. Shrubs are less numerous than in the early woods. Spice bush is typical and paw-paw is limited to the woods edge. In many places bed straw (*Galium alparine* L.) covers the entire floor. This is a vernal plant which by midsummer is reduced to matted stems and innumerable burrs. There are other spring flowers: great white trillium, jack-in-the-pulpit, hepatica, etc. The number of plant species is limited considerably because of lack of light. Moisture is usually constant and abundant, and summer temperature is never extreme. The soil is usually a rich black humus. Leaves cover the ground and large logs are conspicuous. Various niches within the woods may give other habitats. In some places the trees are farther apart and there is more clay in the soil. In others, stream valleys

furnish very moist, well-drained banks. However, there is not the variety of conditions which is found in the oaks.

Under the general substratum conditions, the number of soil-dwelling forms is reduced to a minimum. Most of the species live in logs in some stage of decay, the stage inhabited varying with the species. The number of hypogaeic forms has reached its maximum, whether in response to the reduced light, or because of the increased number of soft, decayed, moist logs, it is impossible to say. Both the number of species and the number of colonies are less than those of the oak woods. This is probably due to the greater constancy of conditions and the lack of variety of habitats. *Lasius niger alienus americanus* and *Aphaenogaster fulva aquia picea* are the only abundant ants in the deep woods. Borders of beech-maple and oak woods are always richest in both species and individuals.

Prairie.—Southwest of Chicago, prairie seems to be the climax plant community instead of forest. Prairies evolve from shallow lakes or marshes, through low prairie characterized by such grasses as *Spartina* and *Calamagrostis,* to climax prairie in which the *Panicum* and *Poa-Andropogon* association is characteristic. Typical plants of the high prairie are the blue stem grasses (*Andropogon* sp.) switch grass (*Panicum virgatum* L.), blue grasses (*Poa* sp.), wild onion (*Allium cernuum* Roth), blazing star (*Liatris spicata* Willd.) and sun flower (*Helianthus* sp.).

In the prairie, ranges of temperature and moisture are as extreme as in the pine dunes. In addition, owing to the nature of the soil, there is apt to be flooding in the spring and more extreme drying out in the summer. Prairie soil is the only habitat and there is little variety in plant food.

The bit of prairie near Chicago is interesting since it is almost a pure *Formica cinerea neocinerea* community. In the high prairie near the Chicago airport, mounds are distributed at no great distance from each other over the entire area. At another location a smaller group of colonies (50 to 75 mounds) is scattered around a marshy pond which dries up in summer. Of the forty-four nests opened, only one was found to contain the slave-making *Polyergus rufescens breviceps.* The *F. cinerea neocinerea* mounds are typically dome-shaped or slightly elongated. The large nests may be twenty-five inches in diameter and from four to six inches high. Occasionally a nest may be found such as one along a ditch slope which was eight feet long and three feet wide. Vigorous nests are usually surrounded by a rim of grass but are entirely bare on top, and have innumerable openings all over the mound.

There are not many other ants which can stand the rigors and lack of habitats of the prairie. *Formica pallide-fulva nitidiventris* and *Lasius niger alienus americanus* are sometimes found.

Succession of Ants in Logs

In the Chicago region there are very few stones, so that ants must rely for their habitats mainly upon soil, or logs, or they may make use of a combination of the two (table I). It will be noted that a large percentage of ants in the beech-maple or oak-maple woods use logs for habitats. This is correlated with two conditions: in the denser woods there are more fallen logs, and the forest floor is not so suitable a habitat as is the more cleared, solid soil of the oaks.

Logs go through characteristic processes of decay, and the characteristic fauna changes with the progressive steps. For convenience the continuous processes of decay has been indicated as representing six stages: *Stage 1.* Tree dead but bark solid; *Stage 2.* Bark loosened, wood solid; *Stage 3.* Sapwood soft, heartwood solid; *Stage 4.* Sap and heartwood soft; *Stage 5.* Beginning to loose shape; *Stage 6.* Merging with the substratum. The distribution of ants through these stages is shown in table I. No ants penetrate into stage one although the *Leptothorax* species may use crevices of solid bark for their nests. Beginning with stage two the widely distributed *Lasius niger alienus americanus* and *Ponera coarctata pennsylvanica* go all the way through. In the harder stages they are found only under the loosened bark. *Aphaenogaster tennesseensis* and the *Camponotus* and *Crematogaster* species seem restricted to rather solid wood. These have their galleries near the surface in hard wood and go deeper as decay progresses. They are not found in the later stages. *Myrmecina graminicola americana* and the yellow *Lasius* species do not come in until the wood is fairly well decayed. Stages three and four reach the climax in both species and numbers. *Aphaenogaster fulva aquia picea* and *Lasius niger alienus americanus* are the most abundant ants in the later stages.

Log succession shows an evolution in miniature where, in general, ants characteristic of more exposed places are found in harder wood and those restricted to more moist conditions live in the more decayed logs. The more widely distributed ants tend to go through a larger series of stages.

Because ants are abundant in every habitat they probably play an important part in the dynamics of succession. The opening up of logs with their galleries so that decay is hastened undoubtedly plays a part in successional changes toward a climax which all woods are approaching. In the early stages of succession ants seem to contribute very little to the hastening of change. In fact, they may retard it by bringing up raw sand or clay to the surface.

Discussion

Table I shows the habitats in which ants have actually been collected. Undoubtedly further collecting would show a larger range on the part of some species. For example, *Stigmatomma pallipes* should occur in the red-white oaks on sand, but since it is a rare ant it has not yet been taken there.

Also, the list is not complete for the area and further collecting should result in the finding of a number of additional species. No indication of abundance of ants is given in the chart. Thus, *Formica fusca subsericea* is listed as occurring all through the sand series as well as on clay and loam. This is true, but the ant is rare on sand while it is one of the most common ants along roadside ditches, and in marshy pastures and woods. For a thorough ecological study of a group, a record of abundance of individuals as well as species is of importance, but this requires special techniques and was not undertaken in this study.

From an ant-distribution viewpoint, the various associes may be designated as ant communities, naming not necessarily the most abundant species, but the ones most restricted to the associes and most characteristic of it.

Fore dunes and poplar dunes: *Pheidole bicarinata* and *Lasius niger neoniger* community.

Pine dunes: *Monomorium minimum* and *Paretrechina* (*N.*) *parvula* community.

Black oak dunes: Community of the *Formica pallide-fulva* subspecies and varieties.

Red-white oak dunes: *Formica truncicola obscuriventris* community.

Mixed oaks on clay: *Prenolepis imparis* and *Leptothorax* spp. community.

Beech-maple climax: *Myrmecina graminicola americana* and *Stenamma brevicorne* community.

Prairie: *Formica cinerea neocinerea* community.

Experiments

Limiting Factors in Distribution

Ants in their distribution, have rather definite and often restricted habitats. The chief factors which may have a general limiting influence are not many. Food, suitable material for a nest, temperature, and moisture seem to be the most important. There may be various other factors such as sunlight, relationship to other ants, etc., which may operate in specific cases. Some ants have a wide range of toleration in regard to each of these, while others are narrowly restricted.

Food is, of course, very important but it is a factor difficult to analyze, because most ants are not restricted to a single type of diet and so may use different foods in different habitats. With ants which depend on aphids for food the relationship to habitat may be secondary, with the toleration of the aphid the limiting factor.

Nesting sites may be specific, or not, depending again on the adaptability of the ant. *Aphaenogaster treatae* and *Iridomyrmex pruinosus analis* seem entirely confined to a sand substratum. Ant mounds are excluded from the dunes. Some of the genus *Camponotus* seem confined to logs. Species

of *Crematogaster* are found in logs where they are available, but will also nest under stones. *Lasius niger alienus americanus* will nest equally readily in logs, under stones, or in soil.

Sunshine may perhaps be a direct factor (Dreyer and Park, '32) in preventing some species from nesting in deep woods, or it may have a secondary effect in that, with lack of sunshine, moisture becomes too great.

Absence of certain other ants is a limiting factor in the case of slave-makers. Thus, since *Polyergus rufescens breviceps* ants must have other species to care for them, they are restricted to places where the slave ants are abundant. The number of slave-maker individuals is also restricted, in that they must be far less abundant in a region than their slaves.

Temperature and moisture seem the most important limiting factors for ants in general. Moisture is probably more important (if the two can be truly separated). Shelford ('13a) says, " A comparison of Fuller's (fig. 1) data with the tables or lists of animals shows that the distribution and succession of animals is clearly correlated with the evaporating power of air." Again he states, " From the standpoint of including many factors, the evaporating power of the air is by far the most inclusive and is therefore by far the best index of physical conditions surrounding animals wholly or partly exposed to the atmosphere."

Assuming that moisture is very important in ant distribution, the problem was set to see whether there were differences in toleration among various species to extremely dry conditions, and whether these differences could be correlated with distribution. In most of the experimental work, *Formica* species were used because these ants meet and withstand extremes of heat and dryness in contrast to other species which stay underground and so avoid the extremes.

Ants were easily kept in good condition in the laboratory by putting them, together with soil of their nests, in large pans with rims of Arctic cup grease around the tops. They were fed on honey and liver with occasional feedings of various kinds of fruits and meats.

Apparatus and Technique

In testing the ants they were subjected to a slow flow of air of specified dryness and temperature. They were kept in these conditions until death occurred.

The apparatus used in testing toleration of various species to low relative humidity at fixed temperatures was similar to that which Pearson ('33) figures and describes. It is placed in a water bath which regulates the temperature. Compressed air is bubbled slowly (two to five liters per minute) through distilled water, then through concentrated sulphuric acid which takes out most of the moisture. From here it is led through a jar containing activated charcoal and glass wool to remove any fumes which might be present,

and then through a bottle of calcium chloride for a final drying before it is led to the jar containing the ants. When higher humidity is desired a stopcock is loosened which allows the dry air to be mixed with that passed through distilled water. The bottle containing the ants is a two liter museum jar sealed with vacuum wax. Within it is placed a hair hygrometer which records temperature as well as relative humidity. Each ant is placed in a separate glass tube 60 mm. long, and with an inside diameter of 8 mm. This gives the ant sufficient space to move about. The two ends are covered with copper mesh which allows a free diffusion of air through the tube. The tubes are strung together and are hung on the back of the hygrometer. Four sets of seven, or twenty-eight such tubes can be included in a jar at one time. Usually two complete experiments of this type were run simultaneously in the water bath and all data from both were combined. The hair hygrometers were checked before each experiment with a wet and dry bulb sling psychrometer.

The ants were placed in the tubes one at a time. Very few were injured by this handling but all the ants were checked before each set was put into the jar. Observations were made every half hour, hour, or three hours according to the length of time of the experiment. Readings were made by taking the jars out of the water bath and looking through the tubes with a reading glass toward an electric light. The jars were never out of the water bath for more than three or four minutes at a time and the temperature deviated very little during that period. Each jar always contained equal numbers of all species tested.

Ants have a characteristic manner of dying. After running about for a time they fall forward, or on one side, and begin twitching their legs. This twitching gradually becomes more feeble until at last it ceases. Immobility—not death—is taken as the end point since there is no way of determining just when death occurs. Ants taken out soon after they have ceased motion can sometimes move their legs slightly, but they do not recover.

Formica Species Used and Their Distribution

For most of the experiments six species of the genus *Formica* were used: (1) *Formica truncicola obscuriventris* seems almost confined to the oak dunes, and there forms nests of anastomosing runways just under the leaf covering; (2) *F. pallide-fulva schaufussi incerta* is also a very common ant at the oak dunes, nesting under bark or logs and having chambers extending down into the sand. It is also found in rather open clay at the borders of fields or in clearings of oak woods; (3) *F. cinerea neocinerea* occurs all through the prairie region, by roadside ditches, around small ponds, and also in the flat dry high prairie; (4) *F. fusca subsericea* is common along roads, at woods edges, or in low marshy fields. The nests always seem to be located where ground water is accessible; (5) *F. sanguinea rubicunda* is not common

but has been found with *F. fusca subsericea* along road ditches or at the edge of oak woods; (6) *F. ulkei* is found at only one place and here the numerous nests are scattered around a shallow pond in an oak woods clearing.

In general, ants 1, 2 and 3 are present in places where fluctuations of temperature and moisture are very great and often severe, while 4, 5 and 6 nest in places where there is a rather constant moisture supply. These environmental differences are indicated in Fuller's table of comparative mean daily evaporation (fig. 1).

Experimental Results

Formica species compared.—The ants were tested with regard to three degrees of severity of dryness and high temperature (table III).

TABLE III. *Average survival time of ants at three degrees of low humidity and high temperature*

Ants	16 ants 30.6 ± .3° C. 12.1 ± 2.7% r. h. Hours Survived	18 ants 34.4 ± .5° C. 9.2 ± 1.5% r. h. Hours Survived	16 ants 41.2 ± .8° C. 8.3 ± .1% r. h. Hours Survived
F. obscuriventris	14.06	10.00	1.93
F. neocinerea	9.50	6.22	1.57
F. incerta	8.12	8.00	1.43
F. rubicunda	6.62	4.94	1.04
F. ulkei	6.18	3.61	.84
F. subsericea	2.81	3.61	.92

Table IV gives these data in full with the duplicate experiments checking the results. It also gives a comparison of each species with every other species and the significance of the difference in survival time between each two as worked out by Student's ('25) method of analysis. By this method, a significance of .0500 means that there are five chances in one hundred of the results being obtained by chance. A figure of .0100 means that there is only one chance in one hundred of random sampling giving the same result. In this work it is considered that a number of .0100 or less indicates that some other factor than chance is responsible for the difference in length of life of any two species. Any figure from this up to .0500 is of border-line significance.

Table V gives significance of the data of experiments 1, 2, and 3 (table IV) and compares each ant with every other ant. Underlining indicates that the difference is considered significant. Where there is not an underlining chance may be responsible for the difference in survival time.

It will be seen from these three tables that *F. truncicola obscuriventris, F. pallide-fulva schaufussi incerta,* and *F. cinerea neocinerea* are definitely able to stand dryness at high temperatures for a longer time than the other three species. This checks very nicely with their distribution as pointed out in an earlier paragraph, i.e., these three species are found in open dunes, fields, or

TABLE IV. *Survival times and significance correlations of ants subjected to dry conditions at high temperatures*

Formica		1. 30.6 ± .3° C. 12.1 ± 2.7% relative humidity 16 ants				1a. 30.1 ± .3° C. 13.2 ± 2.2% relative humidity 15 ants			
a	*b*	hr.a.[1]	hr.b.[1]	diff.	sig.	hr.a.[1]	hr.b.[1]	diff.	sig.
F. obscuriventris	*F. neocinerea*	14.06	9.50	4.56	.0104	—	—	—	—
F. "	*F. incerta*	14.06	8.12	5.94	.0142	—	—	—	—
F. "	*F. rubicunda*	14.06	6.62	7.44	.0000	—	—	—	—
F. "	*F. ulkei*	14.06	6.18	7.88	.0004	—	—	—	—
F. "	*F. subsericea*	14.06	2.81	11.25	.0000	—	—	—	—
F. neocinerea	*F. incerta*	9.50	8.12	1.38	.3824	8.80	6.80	2.00	.1778
F. "	*F. rubicunda*	9.50	6.62	2.88	.0432	8.80	6.06	2.74	.0414
F. "	*F. ulkei*	9.50	6.18	3.32	.0512	8.80	6.86	1.94	.2218
F. "	*F. subsericea*	9.50	2.81	6.69	.0002	8.80	2.53	6.27	.0056
F. incerta	*F. rubicunda*	8.12	6.62	1.50	.1472	6.80	6.06	.74	.4546
F. "	*F. ulkei*	8.12	6.18	1.94	.0938	6.80	6.86	.06	.5916
F. "	*F. subsericea*	8.12	2.81	5.31	.0002	6.80	2.53	4.27	.0000
F. rubicunda	*F. ulkei*	6.62	6.18	.44	.7986	6.06	6.86	.80	.5714
F. "	*F. subsericea*	6.62	2.81	3.81	.0000	6.06	2.53	3.53	.0000
F. ulkei	*F. subsericea*	6.18	2.81	3.37	.0004	6.86	2.53	4.33	.0016

Formica		2. 34.2 ± .5° C. 9.2 ± 1.5% relative humidity 18 ants				2a. 35.3 ± .8° C. 11.0 ± 2.2% relative humidity 16 ants			
a	*b*	hr.a.[1]	hr.b.[1]	diff.	sig.	hr.a.[1]	hr.b.[1]	diff.	sig.
F. obscuriventris	*F. neocinerea*	10.00	6.22	3.78	.0048	—	—	—	—
F. "	*F. incerta*	10.00	8.00	2.00	.1858	—	—	—	—
F. "	*F. rubicunda*	10.00	4.94	5.06	.0004	—	—	—	—
F. "	*F. ulkei*	10.00	3.61	6.39	.0000	—	—	—	—
F. "	*F. subsericea*	10.00	3.61	6.39	.0000	—	—	—	—
F. neocinerea	*F. incerta*	6.22	8.00	1.78	.1332	—	—	—	—
F. "	*F. rubicunda*	6.22	4.94	1.28	.1624	—	—	—	—
F. "	*F. ulkei*	6.22	3.61	2.61	.0034	—	—	—	—
F. "	*F. subsericea*	6.22	3.61	2.61	.0048	—	—	—	—
F. incerta	*F. rubicunda*	8.00	4.94	3.06	.0006	—	—	—	—
F. "	*F. ulkei*	8.00	3.61	4.39	.0008	6.68	4.00	2.68	.0026
F. "	*F. subsericea*	8.00	3.61	4.39	.0000	6.68	3.00	3.68	.0000
F. rubicunda	*F. ulkei*	4.94	3.61	1.33	.0670	—	—	—	—
F. "	*F. subsericea*	4.94	3.61	1.29	.0014	—	—	—	—
F. ulkei	*F. subsericea*	3.61	3.61	0.00	1.0000	4.00	3.00	1.00	.1544

Formica		3. 41.2 ± .8° C. 8.3 ± 1.1% relative humidity 16 ants				3a. 40.7 ± .3° C. 13.5 ± 1.4% relative humidity 12 ants			
a	*b*	hr.a.[1]	hr.b.[1]	diff.	sig.	hr.a.[1]	hr.b.[1]	diff.	sig.
F. obscuriventris	*F. neocinerea*	1.93	1.57	.36	.0962	—	—	—	—
F. "	*F. incerta*	1.93	1.43	.50	.0800	—	—	—	—
F. "	*F. rubicunda*	1.93	1.04	.89	.0016	—	—	—	—
F. "	*F. ulkei*	1.93	.84	1.09	.0000	—	—	—	—
F. "	*F. subsericea*	1.93	.92	1.01	.0004	—	—	—	—
F. neocinerea	*F. incerta*	1.57	1.43	.14	.3766	2.79	1.60	1.19	.0070
F. "	*F. rubicunda*	1.57	1.04	.53	.0038	2.79	1.20	1.59	.0124
F. "	*F. ulkei*	1.57	.84	.73	.0030	2.79	.95	1.84	.0104
F. "	*F. subsericea*	1.57	.92	.65	.0016	2.79	.83	1.96	.0000
F. incerta	*F. rubicunda*	1.43	1.04	.39	.0088	1.60	1.20	.40	.0840
F. "	*F. ulkei*	1.43	.84	.59	.0094	1.60	.95	.65	.0262
F. "	*F. subsericea*	1.43	.92	.51	.0028	1.60	.83	.77	.0262
F. rubicunda	*F. ulkei*	1.04	.84	.20	.2688	1.20	.95	.25	.0954
F. "	*F. subsericea*	1.04	.92	.12	.2932	1.20	.83	.37	.0392
F. ulkei	*F. subsericea*	.84	.92	.08	.5260	.95	.83	.12	.6072

[1] Hr.a. refers to average survival time of ants of column a. (Example: at 30.6° C. and 12.1 per cent relative humidity the average survival time of *F. obscuriventris* was 14.06 hours.) Hr.b. gives similar results for column b.

TABLE V. *Showing significances of differences in survival times*[1]

Formica		30.6° C. 12.1% rel. humid.	34.2° C. 9.2% rel. humid.	41.2° C. 8.3% rel. humid.
F. obscuriventris	*F. incerta*	.0142	.1858	.0800
F. "	*F. neocinerea*	.0104	.0048	.0962
F. "	*F. rubicunda*	.0000	.0004	.0016
F. "	*F. ulkei*	.0004	.0000	.0000
F. "	*F. subsericea*	.0000	.0000	.0004
F. incerta	*F. obscuriventris*	.0142	.1858	.0800
F. "	*F. neocinerea*	.3824	.1332	.3766
F. "	*F. rubicunda*	.1472	.0006	.0088
F. "	*F. ulkei*	.0938	.0008	.0094
F. "	*F. subsericea*	.0002	.0000	.0028
F. neocinerea	*F. obscuriventris*	.0104	.0048	.0962
F. "	*F. incerta*	.3824	.1332	.3766
F. "	*F. rubicunda*	.0432	.1624	.0038
F. "	*F. ulkei*	.0512	.0034	.0030
F. "	*F. subsericea*	.0002	.0048	.0016
F. rubicunda	*F. obscuriventris*	.0000	.0004	.0016
F. "	*F. incerta*	.1472	.0006	.0088
F. "	*F. neocinerea*	.0432	.1624	.0038
F. "	*F. ulkei*	.7986	.0670	.2688
F. "	*F. subsericea*	.0000	.0014	.2932
F. ulkei	*F. obscuriventris*	.0004	.0000	.0000
F. "	*F. incerta*	.0938	.0008	.0094
F. "	*F. neocinerea*	.0512	.0034	.0030
F. "	*F. rubicunda*	.7986	.0670	.2688
F. "	*F. subsericea*	.0004	1.0000	.5260
F. subsericea	*F. obscuriventris*	.0000	.0000	.0004
F. "	*F. incerta*	.0002	.0000	.0028
F. "	*F. neocinerea*	.0002	.0048	.0016
F. "	*F. rubicunda*	.0000	.0014	.2932
F. "	*F. ulkei*	.0004	1.0000	.5260

[1] Numbers underlined are considered to indicate significant differences. For actual survival times in hours consult table IV.

prairie where during the summer drought is often severe, while *F. fusca subsericea, F. sanguinea rubicunda,* and *F. ulkei* occur in places where the water supply is more constant.

Since both relative humidity and temperature were changed for each experiment there was a question whether perhaps temperature and not moisture was the controlling factor. To answer this question a series of experiments was run at 30.4° C. (the same as in experiment 1, table IV) with a higher relative humidity (44.3 per cent).

Table VI shows the results of three combined experiments using forty-two ants of each species. Only four species were available.

TABLE VI. *Average survival time of ants at designated temperature and relative humidity* [1]

		30.4 ± .34° C. and 44.3 ± 1.2% rel. hum.			
		Hours Survived	Hours Survived	Diff.	Sig.
F. incerta	*F. subsericea*	54.49	41.64	12.95	.6912
F. incerta	*F. neocinerea*	54.49	25.35	29.14	.0000
F. incerta	*F. ulkei*	54.49	18.16	36.43	.0000
F. subsericea	*F. neocinerea*	41.64	25.35	16.29	.1224
F. subsericea	*F. ulkei*	41.64	18.16	23.48	.0248
F. neocinerea	*F. ulkei*	25.35	18.16	7.19	.1952

[1] The first column marked "hours survived" refers to the length of life of ants of the first column (thus *F. incerta* lived 54.49 hours) while the second column of figures records survival time of the second column of ants (thus *F. subsericea* averaged 41.64 hours of life).

It will be noted that the ants lived enormously longer at high humidity, and what is more interesting, the relationships between the different species as to length of life changed. *F. fusca subsericea,* which died first under the very dry conditions, lived almost as long as did *F. pallide-fulva schaufussi incerta,* and considerably longer than *F. ulkei.*

Other results not yet fully checked indicate that at the same temperature and still higher relative humidity (70 per cent) *F. fusca subsericea* lives slightly longer than *F. cinerea neocinerea* and *F. ulkei.* Of these, *F. cinerea neocinerea* dies first. Thus, the relationships of the species is just reversed at low and high humidities.

Thus it would seem evident that the ants died differentially in the first experiments as a result of their differences in ability to tolerate low relative humidity and not in response to high temperature. This is at least true at 30° C. and since the relationships are consistent at 30°, 34° and 41° C. it is assumed that at even these higher temperatures the ants died sooner because of dryness.

Other species compared.—The same type of experiment was tried with several other kinds of ants.

(*a*) *Aphaenogaster fulva aquia* is rather common along road and railroad ditches or in open oak woods. Its variety, *A. picea,* occurs in beech-maple woods and especially along moist stream gullies of these woods. These two ants were compared (table VII) because their differences in distribution seem influenced by different moisture optimums. There seems no doubt that there is a definite physiological difference between these two ants with reference to their ability to withstand dryness, and that this difference is correlated with their distribution.

TABLE VII. *Average survival time of Aphaenogaster varieties*

		A. aquia Hours Survived	*A. picea* Hours Survived	Diff.	Sig.
I	21 ants 30.3 ± .2° C. 12.3 ± 1.8% rel. hum.	5.88	3.85	2.03	.0002
II	21 ants 30.0 ± .2° C. 11.5 ± 3.0% rel. hum.	9.97	4.88	5.09	.0000

Comparing *Lasius* species the results are quite different.

(*b*) *Lasius niger neoniger* is most common on the exposed dunes and *Lasius niger alienus americanus* is abundant in deep moist woods, yet their ranges overlap and both are also found in dry pastures which may show as definite lack of water as the dunes. There is no evidence (table VIII) that there is a differential in the toleration of these ants, although the second experiment shows a borderline significance toward *L. americanus* as being the more tolerant of the two. It would seem that the difference in distribution of the two is not a response to dryness. It is interesting to remember in this case that *Lasius niger* varieties do not come out in hot dry weather so they do not face severe conditions.

TABLE VIII. *Average survival time of Lasius subspecies*

		L. neoniger Hours Survived	*L. americanus* Hours Survived	Diff.	Sig.
I	19 ants 30.1 ± .4° C. 17.8 ± 3.3% rel. hum.	4.76	4.37	.19	.8056
II	19 ants 22.7 ± .9° C. 16.7 ± .9% rel. hum.	4.02	5.94	1.92	.0474

(*c*) *Lasius niger alienus americanus* was tested against *L. umbratus mixtus aphidicola,* a hypogoeic species which usually lives in logs in oak and beech-maple woods. In this case also there is no sign of a differential in respect to toleration of low relative humidity.

(*d*) It was found that *Camponotus herculeanus pennsylvanicus* is unique in that it ranges from the most exposed poplar dunes to moist stream valleys in beech-maple woods. Nests of this species were collected and tested from a very moist situation and a very dry one (table IX). There is no indication in this case that the habitat of an individual nest makes a difference in dry toleration within a species.

TABLE IX. *Average survival time of Camponotus herculeanus pennsylvanicus from different habitats*

C. pennsylvanicus	Moist Situation Hours Survived	Dry Situation Hours Survived	Diff.	Sig.
21 ants 30.2 ± .2° C. 12.1 ± 3.0% rel. hum.	44.19	39.47	4.72	.4920

(*e*) The question arose as to whether keeping ants in the laboratory might make some difference in their toleration. In a test with *Formica ulkei* there is no evidence that keeping these ants in the laboratory over winter makes any difference in their reaction to dryness. Neither do ants from different mounds show significant variation.

It seemed interesting to test whether the different castes of a colony would show differential toleration. Experiments testing this were tried with several species.

(*f*) *Camponotus herculeanus pennsylvanicus,* female, worker, and male were tested (table X). It is clear from these two tests that the females are much more resistant than are the workers, and these are in turn more hardy than the males. At higher temperatures the workers begin to loose their superiority to the males. The female is still much more resistant.

TABLE X. *Average survival time of different castes of Camponotus*

Hours Survived	Hours Survived	Difference	Significance
14 ants 30.0 ± .5° C. 12.8 ± 2.4% rel. hum.			
♂—21.35	♀—90.14	68.79	.0000
☿—48.14	♀—90.14	42.00	.0000
♂—21.35	☿—48.14	26.79	.0040
14 ants 30.3 ± .6° C. 11.5 ± 2.5% rel. hum.			
♂—20.71	♀—74.50	53.79	.0000
☿—44.21	♀—74.50	30.29	.0002
♂—20.71	☿—44.21	23.50	.0016

(*g*) *Lasius umbratus mixtus aphidicola,* female, worker, and male were tested. This experiment was run three times (table XI). The females had superior resistance but the results comparing the males and workers were inconclusive.

TABLE XI. *Average survival time of females, workers and males of Lasius*

		Hours Survived	Hours Survived	Diff.	Sig.
I	15 ants 30.2 ± .3° C. 12.1 ± 2.3% rel. hum.	♂—3.90	♀—8.30	4.40	.0000
		☿—3.63	♀—8.30	4.67	.0000
		♂—3.90	☿—3.63	.27	.4488
II	15 ants 30.3 ± .2° C. 13.8 ± 2.3% rel. hum.	♂—4.66	♀—7.90	3.24	.0000
		☿—3.06	♀—7.90	4.84	.0000
		♂—4.66	☿—3.06	1.60	.0086
III	16 ants 30.2 ± .3° C. 13.0 ± 3.9% rel. hum.	♂—5.40	♀—8.53	3.13	.0000
		☿—4.46	♀—8.53	4.07	.0000
		♂—5.40	☿—4.46	.94	.0652

(*h*) *Formica fusca subaenescens* females were tested against the workers of the colony and *Aphaenogaster tennesseensis* females were tested against their workers. In both cases there are again significant differences in favor of the females.

From these tests there is no doubt of the superior resistance of the female, but the results comparing the male and workers are not conclusive. Whether the survival is due to the larger size of the female is not determined. Whatever the cause, there is undoubted survival value for the colony as well as for the female herself. The relationship between the male and workers seems to vary with different species, perhaps in correlation with size differences between the two.

Among the *Formica* species differences in size cannot account for differences in toleration. While the size differences are not great, *F. neocinerea* is a smaller ant than either *F. ulkei* or *F. subsericea.* Nevertheless, under very dry conditions, it lives significantly longer than either of these.

Discussion

Few papers have been found which deal with physiological differences between species of a genus which can be correlated with niches occupied. However, the following three illustrate this type of work.

Parker ('30) worked out the optimum developmental temperatures for three species of grasshoppers of the genus *Melanoplus.* He found that *M. femur-rubrum* had a lower optimum than did *M. mexicanus* or *M. packardi.* Concerning their distribution Parker states, "This species (*M. femur-rubrum*) is most commonly found in bushy areas along streams or in rank-growing grass, while the other species prefer unshaded ground, sparsely covered with vegetation, and are thus adapted to a higher range of temperature."

Shelford ('13b) subjected two salamanders of the genus *Plethodon* to a humidity gradient and found that *P. glutinosus* is more sensitive to dry air than is *P. cinereus.* This is definitely correlated with habitat differences as *P. glutinosus* lives in damper places than does *P. cinereus.* The results are especially interesting in that *P. cinereus* is the smaller animal and its evaporating surface per unit weight would be greater for that reason.

Williams ('34) experimented with two species of termites, *Reticulitermes hesperus,* characteristic of more moist regions, and *R. tibialis* of more arid places. He found that *R. tibialis* could live with slightly less moisture in the soil than could *R. hesperus.* He also discovered that *R. hesperus* could tolerate a greater amount of carbon dioxide which is correlated with high moisture content. He says, "Thus both low and high soil moisture contents appear to serve as controlling factors in the distribution of these two subterranean termites."

It is established in the preceding pages that there are definite physiological

differences between *Formica* species living in dryer situations and those inhabiting more moist places. In general, differences between species are usually considered nonadaptive, and are explained on the basis of isolating factors, but in these cases the physiological differences appear definitely adaptive in that they are correlated with the type of habitat which the animal can utilize.

Summary

1. Seventy species, subspecies, and varieties of ants were collected within a radius of ninety miles of Chicago.

2. Records were kept showing their distribution through the following ecological stages: (*a*) beach; (*b*) fore dunes; (*c*) poplar dunes; (*d*) pine dunes; (*e*) black oak dunes; (*f*) red-white oak dunes; (*g*) mixed oak woods on clay; (*h*) oak-maple woods on sand; (*i*) beech-maple climax; and (*j*) prairie.

3. It was found that species reached their peak of abundance in the oaks on clay. This was correlated with diversity of habitats in that associes, and with lack of extreme temperature or dryness.

4. Few species are restricted to sand although some are much more abundant there. In contrast, sand seems a limiting factor in many species.

5. A definite succession of species through stages in decaying logs was found. This correlates in a broad way with general distribution of the ants, those of the less exposed places being restricted to the later stages of decay.

6. From distribution studies it seemed probable that toleration or lack of toleration to extremes of dryness is one of the important differentiating factors in the distribution of species, allowing some forms to penetrate into places of low relative humidity where others are excluded.

7. To test this observation experimentally six species of the genus *Formica* were subjected to controlled conditions of dryness. It was found that those living in the drier places (black oak dunes, prairie, etc.) were more resistant to dryness than those living where the moisture supply is more constant.

8. For species of *Lasius* no such differentiation to dryness could be found. These ants do not forage on hot dry days and so do not face extremes to the extent that the *Formica* ants do.

9. In all cases tested females lived much longer under dry conditions than did workers or males of the same colony. This may be due to superior size. In any case it should be of survival value to the colony in that the isolated female may be subjected to severe conditions when founding her colony.

10. Variations in the survival times among various species of *Formica* demonstrate physiological differences between the species living in moist places and those of dryer situations. These differences are probably adaptive in that they are correlated with the ability of the species to penetrate niches where the moisture supply may be very low at times.

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LANCASTER PRESS, INC., LANCASTER, PA.